



## **Dominance Orders in Animal Societies: The Self-organization Hypothesis Revisited**

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In previous papers (Theraulaz *et al.*, 1995; Bonabeau *et al.*, 1996) we suggested, following Hogeweg and Hesper (1983, 1985), that the formation of dominance orders in animal societies could result from a self-organizing process involving a double reinforcement mechanism: winners reinforce their probability of winning and losers reinforce their probability of losing. This assumption, and subsequent models relying on it, were based on empirical data on primitively eusocial wasps (*Polistes dominulus*). By reanalysing some of the experimental data that was previously thought to be irrelevant, we show that it is impossible to distinguish this assumption from a competing assumption based on preexisting differences among individuals. We propose experiments to help discriminate between the two assumptions and their corresponding models—the self-organization model and the correlational model. We urge other researchers to be cautious when interpreting their dominance data with the 'self-organization mindset'; in particular, 'winner and loser effects', which are often considered to give support to the self-organization assumption, are equally consistent with the correlational assumption.

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### **1. INTRODUCTION**

Animals that live in group may benefit from reduced predation risk, easier access to food, increased *per capita* productivity, availability of mates, or any combination

of these factors. But conflict may result from group living because of increased competition over critical resources. In many species of animals, when several unacquainted individuals are placed together in a group, they engage in (usually pairwise) contests for dominance. Some of the contests are violent fights, some are fights that do not lead to any serious injury, and some are limited to the passive recognition of a dominant and a subordinate. For an initial period ranging from hours to weeks, depending upon such factors as group size and species of animals, contests will be extremely frequent, before becoming less and less frequent and being replaced by stable dominance–subordination relations among all group members (Chase, 1974; Wilson, 1975). The larger the group, the longer it takes for the relations to settle. Once they are settled, they usually last for long periods of time, with few, generally unsuccessful, attempts by subordinates to take over. When such a network of dominance–submission relationships, a hierarchy, arises in a stable group, it organizes the group in such a way that conflicts do not completely offset the advantages of group living.

Dominance behavior has been described in hens [e.g., Schjelderup-Ebbe (1913, 1922); Allee (1942, 1951, 1952); Guhl (1968)], cows [e.g., Schein and Fohrman (1955); Barton *et al.* (1974)], ponies [e.g., Tyler (1972)], fish [e.g., Lowe (1956); Bovbjerg (1956); Bovbjerg and Stephen (1971); Wilson (1975)], in crabs, lobsters, and crayfish (Jachowsky, 1974; Glass and Huntingford, 1988; Huber and Kravitz, 1995), lizards Evans (1951, 1953), frogs when they are crowded together [e.g., Haubrich (1961); Boice and Witter (1969)], rats [e.g., Van de Poll *et al.* (1982)], primates [e.g., Kummer (1968); Baldwin (1971); Candland and Leshner (1971); Mendoza and Barchas (1983); Thierry (1985)], or social insects Wilson (1971), especially in wasps [e.g., Gervet (1962, 1964); Pardi (1942, 1946, 1948); West Eberhard (1969); Evans and Eberhard (1970); Röseler *et al.* (1986); Röseler (1991); Theraulaz *et al.* (1992)], ants [e.g., Cole (1981); Franks and Scovell (1983); Heinze (1990); Heinze *et al.* (1994); Bourke (1988); Oliveira and Hölldobler (1990); Medeiros *et al.* (1992)], and bumblebees [e.g., Van Honk and Hogeweg (1981)]. In social wasps, dominance hierarchies are more widespread than originally thought; in particular, dominance behavior is not limited to the conspicuous overt dominance observed in *Polistes dominulus*, but includes more subtle forms of dominance through chemical interactions (Jeanne, 1991). This list is far from being complete: the literature on dominance orders contains hundreds of references dating back to the first systematic investigations of Schjelderup-Ebbe (Schjelderup-Ebbe, 1913, 1922) on the domestic fowl *Gallus domesticus*.

One of the questions that one may ask about dominance orders is: how do they form? In an attempt to answer this question, we suggested in several previous papers (Theraulaz *et al.*, 1995; Bonabeau *et al.*, 1996), following Hogeweg and Hesper (1983, 1985), that the formation of dominance orders in animal societies could result from a self-organizing process involving a double reinforcement mechanism: winners reinforce their probability of winning and losers reinforce their probability of losing. This assumption, and subsequent mathematical and computer models

relying on it, were based mostly on empirical data on primitively eusocial wasps (*Polistes dominulus*) (Theraulaz, 1991; Theraulaz *et al.*, 1989, 1990, 1991, 1992). We suggest in this paper that another alternative explanation is equally consistent with the empirical data, especially after taking into account some of the empirical data that was previously discarded because it did not seem to be relevant to explain the formation of dominance orders. The alternative model is based not on a reinforcement process but on preexisting differences between individuals; that is, differences that exist before the formation of the group. It is also called the correlational model (Chase, 1986). After thoroughly reviewing the empirical data (Section 2) and presenting the two models together with a careful discussion of their underlying assumptions (Section 3), we conclude that it is not possible, on the sole basis of the current empirical data, to tell which assumption is right. We propose experiments that could help discriminate between the two competing assumptions (Section 4).

## 2. DOMINANCE ORDERS IN THE PRIMITIVELY EUSOCIAL WASP *Polistes dominulus*

**2.1. Preliminaries.** The primitively eusocial paper wasp *Polistes dominulus* (formerly *Polistes gallicus*) is a common wasp native to temperate regions of Europe. In *Polistes dominulus*, which has an annual cycle, overwintered females often cooperate in the founding of colonies in the spring. These females, the foundresses, form associations characterized by a linear dominance hierarchy (Pardi, 1942, 1946, 1948; Gervet, 1962, 1964; Röseler, 1991). In a linear dominance hierarchy, the dominant female, also called  $\alpha$ -female, is dominant over all other females. The second-in-rank female, the  $\beta$ -female, is dominant over all females other than the  $\alpha$ -female. And so forth to the bottom of the hierarchy ( $\alpha > \beta > \gamma > \dots$ ), where the lowest-ranking female is dominated by all other females. Although any overwintered female is able to found its own nest, the  $\alpha$ -female becomes the principal egg layer of the colony. The aggressive behavior of the  $\alpha$ -female toward the other foundresses causes their ovaries to regress (Pardi, 1946; Deleurance, 1946) and they take on the roles of workers for the colony. Other females may lay fewer eggs, all or most of which are eaten by the dominant: this phenomenon, first observed by Heldmann (1936), was called differential oophagy by Gervet (1964). The  $\alpha$ -female recognizes the eggs laid by her subordinates and eats them within a day after they are laid (Gervet, 1964).

The dominance hierarchy is established through aggressive interactions among foundresses within the first days of colony foundation. The intensity of these interactions decreases with time, from severe fights when the females meet for the first time to the simple recognition of a dominant by a subordinate after several days. The resulting hierarchical organization determines not only the partitioning of reproduction but also the division of labor among nestmates. The dominant

female remains on the nest where she lays eggs and contributes to nest building, while the other females perform the other tasks, especially the tasks outside the nest. Although division of labor will not be discussed in this chapter, it is clear that the reproductive success of a social insect colony depends on the efficiency of its mechanism for task allocation. In *Polistes dominulus*, task allocation is coupled with the hierarchical organization (Theraulaz *et al.*, 1990, 1992).

In social insects, paper wasps *Polistes dominulus* have played an important role in the study of dominance hierarchies and in the development of a methodology to characterize dominance hierarchies (Heldmann, 1936; Pardi, 1942, 1946, 1948). Foundress associations of *Polistes dominulus* usually contain a small number of individuals, between one and ten. Hierarchical interactions are more or less ritualized pairwise contests, during which a female physically dominates another female. Let us at this point distinguish *social* or *behavioral* dominance from *reproductive* dominance. While behavioral dominance has to do with physical dominance behavior, reproductive dominance is related to the partitioning of reproduction. Although these two forms of dominance are almost always associated since the physically dominant female is also the one that monopolizes reproduction in normal conditions, they can be distinguished experimentally. Ovariectomized foundresses of *Polistes dominulus* can still become and remain behaviorally dominant, but cannot lay eggs. The  $\beta$ -female then becomes the principal egg layer and her eggs are tolerated by the  $\alpha$ -female (Röseler *et al.*, 1985; Röseler and Röseler, 1989). The  $\alpha$ -female is socially or behaviorally dominant while the  $\beta$ -female achieves reproductive dominance (Röseler, 1991). As will be discussed in Section 2.3, the physiological correlates of both types of dominance are tightly coupled, but it is not clear how exactly they interact.

## 2.2. Formation and characterization of the hierarchical structure.

2.2.1. *Dominance index.* Rank is not enough to characterize hierarchical activity because it does not consider the number of interactions, dominances, and subordinations in which an individual has been involved. In order to characterize the dominance order of a group of *Polistes dominulus*, Pardi (1946, 1948) introduced a variable that can be measured in experiments: the dominance index  $X$  of an individual, defined by  $X = D/(D + S)$ , where  $D$  is the number of times that the individual has been dominant in pairwise contests since the formation of the group, and  $S$  is the number of times that the individual has been defeated since the formation of the group.  $X$  is therefore the proportion of successful contests with respect to the total number of interactions  $D + S$ . The dominance index is used to define the hierarchical rank of an individual:  $X = 1$  when all contests have been won, and  $X = 0$  when all contests have been lost. The function that gives  $X$  as a function of rank is called *hierarchical profile*.

$X$  is a biased measure of an individual's hierarchical activity: for example, it does not give enough weight to the individual's total number of interactions (an

individual that has been involved in only one, successful, contest is characterized by  $X = 1$ ), it does not include the identity of the individuals with which interactions have taken place (some pairs of individuals may have frequent interactions while other pairs only rarely interact), or it gives as much weight to recent contests as to contests that took place a long time ago. However, these biases do not seem to affect the value of  $X$  as an indicator of hierarchical activity in *Polistes dominulus*. The biases mentioned above are limited because the hierarchical profile quickly stabilizes after all possible pairwise interactions have taken place at least once.

*2.2.2. Experimental setup.* We now describe laboratory experiments that were undertaken to understand the formation of the dominance order in *Polistes dominulus* (Theraulaz, 1991; Theraulaz *et al.*, 1989, 1990, 1991, 1992). Queens were collected in the Marseille area (south of France) during hibernation, in December 1987 and January 1988, and placed in a room at a temperature 10° C. Starting on the first of March 1988, they were placed in groups of five in transparent plastic cages (16 × 19 × 24 cm) at a mean temperature of 27 °C, and provided with prey (caterpillars), blotting paper, water, and sugar. The cages were continuously refilled with a sufficiently large amount of food, but not directly on the nest so that foraging was necessary to obtain the food. Light was provided for 12 h every day (from 6:00 am to 6:00 pm). As soon as the first nest was founded, surplus individuals were removed so that only monogynous colonies could develop. At emergence, each wasp was individually marked. The total number of females was kept at 13 by removing additional females, and all males were removed, so as to eliminate the effects of group size and the presence of males on the establishment and maintenance of social interactions. At the beginning of the experiment, each colony therefore consisted of one foundress and the first 12 newly-emerged females. In two control nests, no intervention took place apart from replacing dead females. In two experimental nests, the first queen was removed after 5 days, and the subsequent  $\alpha$ -females were systematically removed every 8 days, five times in a row. Eight days were assumed to be sufficient for a new hierarchy to establish and settle. The two experimental colonies provided 10 experimental conditions to study the formation of the hierarchy.

The females were observed for 4 hours per day (2 × 2 hours), in 10 series of 1-week observations. Thirty-one behavioral items were recorded. The dominance index  $X = D/(D + S)$  was computed after observation of the outcomes of individual encounters [dominance ( $D$ ) or subordination ( $S$ )], using standard cues to identify the winner and the loser of a hierarchical interaction (Pardi, 1942, 1946, 1948; Gervet, 1964; Reeve, 1991; Röseler, 1991; Theraulaz *et al.*, 1992). At first contact, two females intensively antennate one another and begin to fight, straightening up, grappling with their forelegs, and attempting to bite one another. After such a fight, one of the females escapes or adopts a subordinate posture in which she remains motionless, antennae and head lowered, while the dominant climbs on her body and intensively antennates and mouths her. In subsequent encounters, the

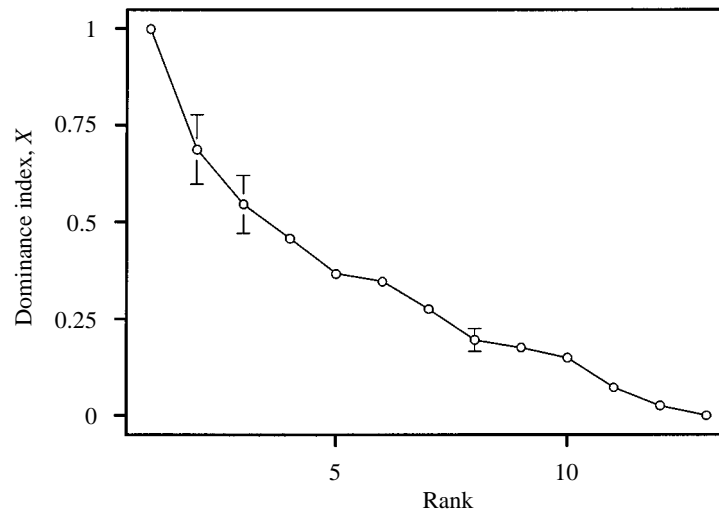


Figure 1. Dominance index as a function of rank in *P. dominulus*. Sample size: 10 experimental colonies of 13 individuals. After Theraulaz (1991).

subordinate female has a crouching posture, with antennae lowered, and sometimes spontaneously regurgitate fluid. When the hierarchy is settled, the interactions between a dominant and a subordinate are often limited to avoidance behavior from the subordinate. Abdominal wagging, a short-period vibration of the gaster from side-to-side (Reeve, 1991), is sometimes associated with dominance behavior during antenation of a subordinate by a dominant, but is also performed during cell inspection and it has recently been suggested that it plays a role in adult larva communication (Savoyard *et al.*, 1999).

Figure 1 shows the dominance index  $X$  as a function of rank, the colony's hierarchical profile, averaged over 10 experiments. The profile is remarkably stable under fixed experimental conditions. There is little variance among the 10 profiles obtained experimentally. In all experiments, older wasps, that had spent more time on the nest, became dominant, and more generally rank reflected the order in which the females were introduced into the nest.

**2.2.3. Probability of interaction.** The frequency and intensity of the aggressive interactions vary with hierarchical rank. In particular, as was established by Pardi (1946, 1948) [see also Theraulaz *et al.* (1989, 1992)], the stronger individuals of a hierarchy tend to interact more frequently than others. Figure 2 shows the percentage of all dominances and subordinations accounted for by each individual as a function of the individual's rank. The percentage of dominances is characterized by a rapid decay as a function of rank, from 47% for the  $\alpha$ -female to 0% for the female at the bottom of the hierarchy. The percentage of subordinations is first increasing and then decreasing as a function of rank: this is because lower-ranking individuals, although they are almost always defeated, are involved in few interactions (see Fig. 3).

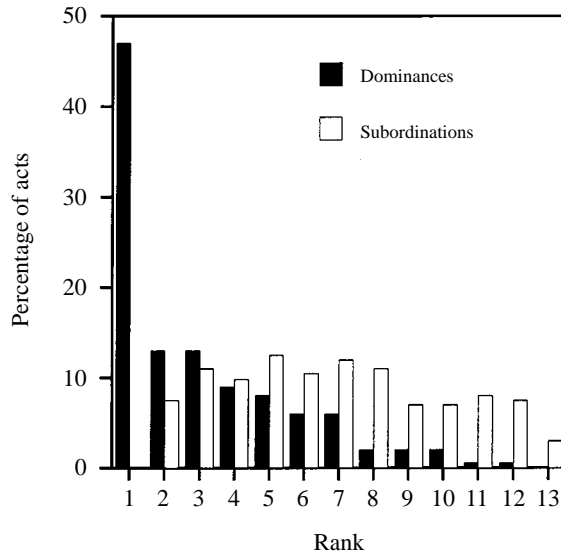


Figure 2. Proportion of dominances and subordinations as a function of hierarchical rank in a colony of *P. dominulus*. Sample size: 10 experimental colonies of 13 individuals. Error bars are not shown. After Theraulaz (1991).

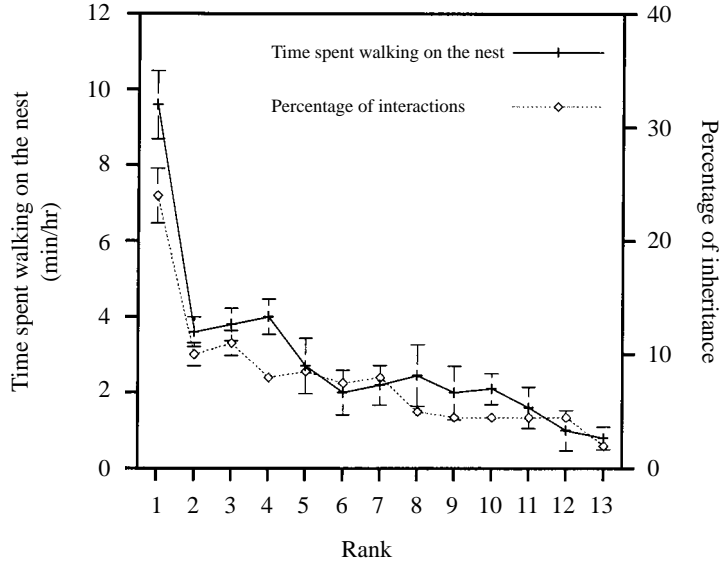


Figure 3. Fraction of interactions  $PI(R)$  involving an individual and time  $T(R)$  spent walking on the nest as a function of rank  $R$ . The best fit to  $PI(R)$  is given by  $23.03 \times R^{-0.721}$  (df. = 128,  $r = 0.918$ ), whereas the best fit to  $T(R)$  is given by  $8.9 \times R^{-0.758}$  (df. = 128,  $r = 0.918$ ). Sample size: 10 experimental colonies of 13 individuals. After Theraulaz (1991).

Several factors may explain the differential probability of interaction observed in the experiments:

- It may be due to motivational differences resulting from neurophysiological factors associated with dominance. Indeed, when two individuals meet, the initiative to interact is usually taken by the higher ranking of the two. Conversely, the motivation of a subordinate to engage in a contest with a dominant may be weak.
- It may also result from the fact that the dominance order is tightly coupled with the division of labor in the colony: the  $\alpha$ -female spends most of the time on the nest (more precisely, on the nest face), where dominance interactions take place, whereas other females, acting as workers for the colony, frequently leave the nest to retrieve food and water, and have fewer opportunities to interact.
- The differential probability of interaction may also result from the increased mobility on the nest of the more dominant females, especially the  $\alpha$ -female: an individual that moves more per unit time has more opportunities to interact.

Let  $T(R)$  be the total time spent walking on the nest by an individual of rank  $R$ , and  $T(X) = T(X(R))$  the total time spent walking on the nest by an individual of dominance index  $X$ . Figure 3 shows  $T(R)$  and the percentage of all interactions,  $PI(R)$ , in which each individual was involved as a function of rank:  $T(R)$  and  $PI(R)$ , although represented at different scales, clearly have similar shapes. One may therefore assume that the probability for an individual to interact with any other individual is proportional to the time  $T$  it spends walking on the nest. This assumption is simple, but  $T$  results from complex factors such as those mentioned above: motivation, spatial location, and mobility. The best fit to  $PI(R)$  is given by  $23.03 \times R^{-0.721}$  (df. = 128,  $r = 0.918$ ), whereas the best fit to  $T(R)$  is given by  $8.9 \times R^{-0.758}$  (df. = 128,  $r = 0.918$ ).

In addition, there seems to be also a well-defined relationship between the dominance index  $X$  and  $T$ . Figure 4 shows that  $T(X)$  increases in an exponential-like manner as a function of the dominance index. The best fit to the data is  $T(X) = 1.32 \times 10^{0.836X}$  (df. = 128,  $r = 0.944$ ). Each point in Fig. 4 represents the average  $T(X(R))$ , and error bars are given for both  $T$  and  $X$ : error bars in the  $y$ -direction correspond to the standard deviation of  $T$  over 10 experiments, whereas error bars in the  $x$ -direction correspond to the standard deviation of  $X$  over 10 experiments for individuals of a given rank. The fit obtained for  $T(X)$  is slightly better than for  $PI(R)$  or  $T(R)$ , suggesting that  $T$  may be determined by the dominance index  $X$  rather than by the rank  $R$  alone (again, the dominance index contains more information about the hierarchical status of an individual than simply its rank).

**2.2.4. Removal of the  $\alpha$ -female.** When the  $\alpha$ -female is removed from a group and replaced with a newly-emerged individual, a burst of hierarchical activity is observed. The hierarchical profile, involving the remaining individuals, obtained

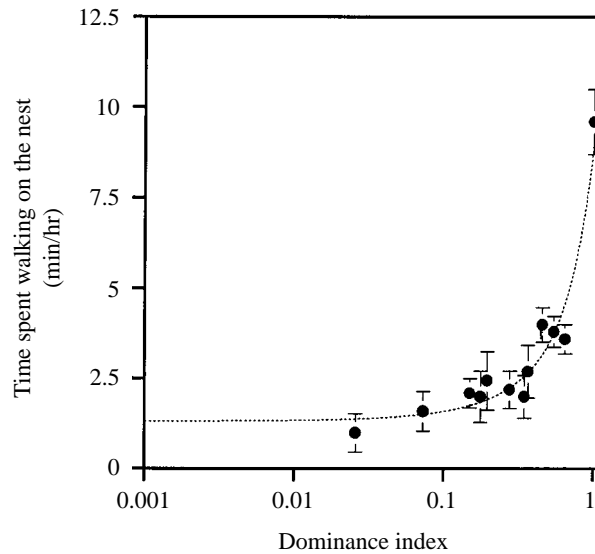


Figure 4. Time per hour spent walking on the nest as a function of the dominance index  $X$ . The dashed curve represents the best exponential fit ( $T(X) = 1.32 \times 10^{0.836X}$ ,  $df. = 128$ ,  $r = 0.944$ ). Sample size: 10 experimental colonies of 13 individuals. After Theraulaz (1991).

after this burst of interactions is exactly similar to the one observed before the perturbation (Theraulaz *et al.*, 1989, 1992). The mean number of hierarchical interactions per unit time in the perturbed colonies is significantly larger than in the control colonies, especially for the top individuals of the new hierarchy. The new  $\alpha$ -female accounts for 45% of all the dominance scenes recorded in these bursts of hierarchical activity, while the immediate subordinate individuals newly promoted to ranks 2 to 4 account for approximately 35% of these scenes. In addition, the time  $T$  spent walking on the nest increases when individuals reach a higher rank. Figure 5 shows the difference between the values of  $T$  after and before reaching a higher rank, as a function of the rank reached.

**2.3. Determinants of dominance in *Polistes dominulus*.** The determinants of dominance in social wasps in general, and *Polistes dominulus* in particular, are remarkably surveyed by Röseler (1991). Pardi (1946) was the first to seek a physiological basis for dominance behavior. He observed that the  $\alpha$ -female has well-developed ovaries, and that egg-formation, oogenesis, is inhibited in subordinates. The lower in the hierarchy, the more oogenesis is inhibited. Oogenesis is correlated with high titers of two hormones in the hemolymph (the equivalent of our blood): the juvenile hormone (JH) produced by the corpora allata (CA), and ecdysteroids produced by the ovaries (Röseler *et al.*, 1980, 1984; Turillazzi *et al.*, 1982). The CA are a pair of small compact glands of tightly packed cells located in the neck region and connected to the brain by a nerve (Nijhout, 1994). The synthetic activity

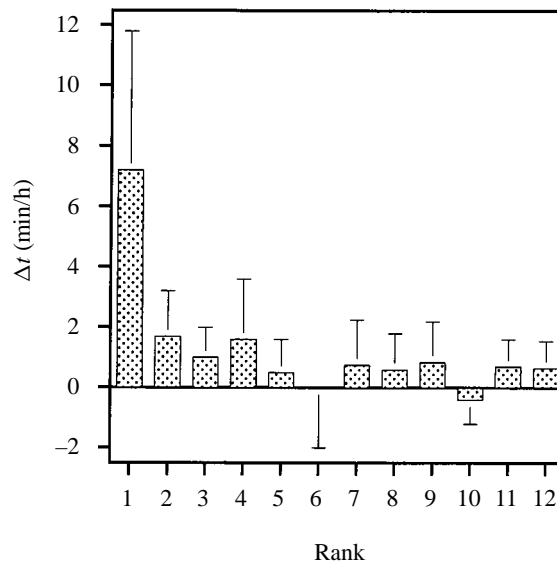


Figure 5. Difference between the values of the time  $T$  spent walking on the nest after and before reaching a higher rank, as a function of the rank reached. Sample size: nine experimental colonies of 12 individuals. After Theraulaz (1991).

of the CA is lower in subordinates than in dominant females (Röseler *et al.*, 1980), resulting in lower JH titers in the hemolymph. The size of the CA in subordinates is also smaller (Röseler *et al.*, 1984, 1985). Once the hierarchy is settled, oogenesis and endocrine activity become high in the dominant female, and progressively decrease in subordinates. A good survey of the nature and role of insect hormones can be found in Nijhout (1994).

The role of JH and ecdysteroids was further demonstrated by hormone treatment (Röseler *et al.*, 1984). More foundresses with relatively small CA and oocytes became dominant after they had been injected with juvenile hormone (JH I) or ecdysteroids (20-hydroxyecdysone), or both simultaneously, than did controls (Röseler *et al.*, 1984; Röseler, 1991). The two hormones do not have additive effects (injection of both hormones does not yield significantly different results than injection of a single hormone), but when the titer of one of these hormones is low, but not too low, it can be compensated for by the other hormone to achieve dominance. When the CA activity is very low, as is the case in parasitized wasps, injection of ecdysteroids is not sufficient to achieve dominance. The interaction between the two types of hormones is not clear. In ovariectomized foundresses, the ecdysteroids titers are low, but they can still achieve dominance if their CA activity and JH titers are high (Röseler *et al.*, 1985). Dominance behavior is more strongly associated with the activity of CA than in unmutated females. These results suggest that both JH and ecdysteroids influence dominance behavior directly. JH is sufficient to induce dominant behavior in ovariectomized foundresses, and is believed to stimulate the production of ecdysteroids in unmutated foundresses. On the other hand,

ecdysteroids alone are also sufficient to induce dominant behavior. Ecdysteroids may also be responsible for aggressive behavior, although it has not been shown in *Polistes dominulus*: aggressive workers in honeybees have more developed ovaries than less aggressive workers, but not as developed as egg-laying workers (Velthuis, 1976).

The endocrine activity of the  $\alpha$ -,  $\beta$ -, and  $\gamma$ -females is greater in the presence of more subordinates, and the synthetic activity of the CA is greater in the  $\alpha$ -female of a multiple-foundress association than in a lone foundress, suggesting that interactions with subordinates promote endocrine activity and possibly reinforce the hierarchical status of dominant individuals (Röseler *et al.*, 1984). Similar results were obtained by Turillazzi *et al.* (1982). The basis for this observation may be that  $\beta$ -females in two-foundress associations cannot dominate subordinates and exploit them by forcing them to forage and obtain food from them. Moreover, a  $\beta$ -female in a larger group of foundresses experiences less subordinations, since domination by the  $\alpha$ -female, which is responsible for a large portion of the interactions, is shared by all subordinates.

Hierarchical interactions not only inhibit oogenesis and endocrine activity in subordinates, they also amplify the reproductive physiology of the dominant females. Another factor, related to division of labor, may further amplify differences in reproductive abilities between dominant and subordinate females. Subordinates often leave the nest to forage: foraging flights are energy expensive, and may slow down oogenesis. Moreover, the dominant female frequently receives food from her subordinates.

Body size has been found to play a role in determining the outcome of an encounter: a large female is favored in aggressive interactions. But the dominant foundress is not always the largest female in the association. Turillazzi and Pardi (1977) showed that 30% of *Polistes dominulus* associations are dominated by a female which is not the largest one. It seems that the influence of body size is mainly due to a relation between large size and high endocrine activity (Turillazzi and Pardi, 1977; Noonan, 1981; Dropkin and Gamboa, 1981).

Most measurements of endocrine activity, CA size, and ovarian development have been performed after the establishment of the hierarchy. But are all females identical at first contact with respect to these factors, or are they already differentiated? Experiments by Röseler *et al.* (1985) show that after hibernation, foundresses are not physiologically equal. Pairwise relationships between females were formed just after hibernation, and morphological and physiological measurements were made right after the first relationship. It was found that size did not play any significant role in determining the rank of a female, but that 91% and 83% of the females that became dominant had larger CA and oocytes than their subordinates. When foundresses in a group were tested in pairs, the resulting hierarchy reflected the volume of their CA. Figure 6 shows the volume of the CA of differently ranked foundresses at the time of the establishment of the dominance order in four-foundress associations (Röseler, 1991).

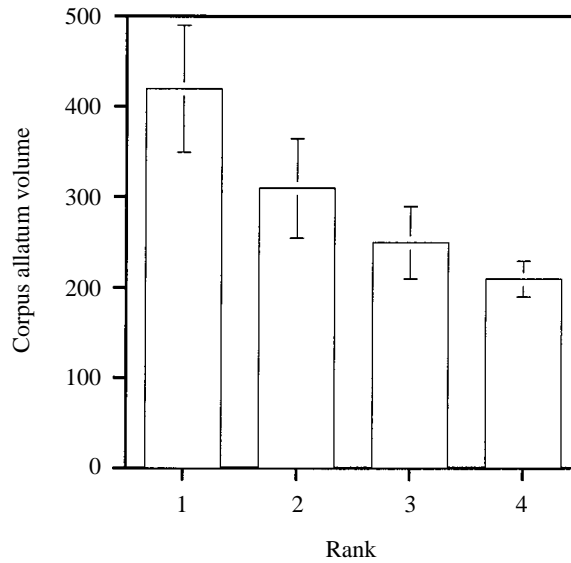


Figure 6. Volume of the CA of differently ranked foundresses at the time of the establishment of the dominance order in four-foundress associations. Sample size: eight for ranks 1, 2, and 3, and six for rank 4. Modified from Röseler (1991, Fig. 9.3, p. 328).

Differences in endocrine activity and ovarian development, and therefore in the ability to exhibit dominant behavior, exist at the end of hibernation, even between individuals from the same hibernation site (Röseler, 1985). This initial differentiation results from asynchrony in emergence from hibernation, and differential exposure to environmental signals. The first foundress of a group often achieves dominance, but this may be due to a higher endocrine activity of females that leave hibernation early, or to a progressive increase of the endocrine activity after hibernation in the absence of any interaction with other females, or to a 'prior residence' effect whereby females which are familiar with a nest or a location more easily achieve dominance. Moreover, it is not clear whether females that leave hibernation early have a higher endocrine activity, or if females with a higher endocrine activity tend to leave hibernation early. Some foundresses may have an inherently higher endocrine activity resulting from a combination of factors, including genotype, feeding during development, or other environmental variations. The disadvantage of emerging late, with lower endocrine activity and smaller CA than potential cofoundresses, decreases within a few days if the female has not been dominated, suggesting that being dominated prevents CA from growing and decreases the endocrine activity related to dominance. This also indicates that the endocrine activity increases naturally after hibernation in the absence of interactions.

### 3. MODELS

#### 3.1. *Self-organization.*

3.1.1. *Introduction.* The model presented in this section (Hogeweg and Hesper, 1983, 1985; Jäger and Segel, 1992; Theraulaz *et al.*, 1995; Bonabeau *et al.*, 1996) makes several assumptions about the dynamics of hierarchy formation. These assumptions are described in detail in Box 1: *these assumptions do not involve the time spent by each individual walking on the nest*, as this data did not seem to be relevant (Bonabeau *et al.*, 1996) although it obviously influences the rate of interaction of individuals. We will introduce in Section 3.2 a competing model that takes this data into account.

The self-organization model relies on a simple fundamental hypothesis, initially introduced by Chase (1982a,b): an individual that wins (respectively loses) a contest is more likely to win (respectively lose) subsequent contests. Assume that all individuals are initially almost equally likely to win contests. The outcomes of the first contests are relatively unpredictable, because either individual in a pairwise contest can win. But as the number of interactions increases, individuals progressively differentiate: those that won the first contests are more likely to win future contests, whereas those that lost the first fights are unlikely to make it to the top. This reinforcement mechanism:

- amplifies small initial differences between individuals,
- generates a group of differentiated individuals, a social structure, out of an initially homogeneous group.

Such ‘loser and winner effects’ (Chase, 1982a,b, 1985, 1986; Chase and Rohwer, 1987), in which an individual which is observed to dominate in one contest is more likely to be observed to dominate in a subsequent contest, have been reported in chickens (McBride, 1958; Chase, 1980, 1982a,b, 1985), crickets (Alexander, 1961; Burk, 1979), fish (Francis, 1983; Beaugrand and Zayan, 1984), mice (Ginsburg and Allee, 1975), rats (Van de Poll *et al.*, 1982), rhesus monkeys (Mendoza and Barchas, 1983; Barchas and Mendoza, 1984), bumblebees (Van Honk and Hogeweg, 1981), wasps (Theraulaz *et al.*, 1989, 1992), and more recently crayfish (Gössmann and Huber, 1999).

However, the observation of apparent winner–loser effects can result from initial differences between individuals (Slater, 1986): if the ‘strength’ or ‘force’ of an individual is an intrinsic property or advantage of that individual that is more or less conserved over time and if unacquainted individuals with different forces are put together, the strongest individual wins its first contest and all subsequent contests, whereas the weakest individual loses its first contest and all subsequent contests. Winner–loser effects are indeed observed, but they do not result from a reinforcement. A model based on intrinsic preexisting differences between individuals is called the *correlational model* (Chase, 1986). In Section 3.2, we will test whether a

**Box 1****Assumptions of the self-organization model**

- (1) Each individual is characterized by a force  $F$ , which influences its ability to win contests.  $F$  reflects endocrine activity, ovarian development, and other factors.
- (2) Individuals have initially identical or almost identical forces. That is rarely true in nature, but could be approached in the laboratory.
- (3) Individual recognition, if it exists, plays no role in the outcome of a contest. In other words, the force of an individual does not depend on which other individual it is encountering.
- (4) A pairwise contest between  $i$  and  $j$  is won by  $i$  with a probability which is given by a rapidly increasing function of the difference between the force  $F_i$  of  $i$  and the force  $F_j$  of  $j$ . If  $i$  and  $j$  have equal forces, the probability that  $i$  wins is  $1/2$ . If  $F_i$  is larger than  $F_j$ ,  $i$  wins almost certainly. Otherwise,  $i$  loses. The outcome of a contest is probabilistic because reversals of dominance can occur. But such reversals are highly unlikely after some time, so that the outcome should be almost deterministic (rapid increase as a function of  $F_i - F_j$ ).
- (5) When  $i$  wins,  $F_i$  increases. When  $i$  loses,  $F_i$  decreases. This assumption relies on three observations: (a) the ovaries of the dominant females develop, whereas those of the subordinates regress. (b) Ovarian development is induced by JH and generates an increase of ecdysteroids in the hemolymph. Both hormones increase the probability of dominating. (c) More interactions with subordinates increases endocrine activity. The opposite is at least to some extent true, since lone foundresses reproduce, whereas they may not reproduce if they are subordinates in a group. Also, the disadvantage of emerging late, with lower endocrine activity and smaller CA than potential cofoundresses, decreases within a few days if the female has not been dominated, suggesting that being dominated prevents CA from growing and decreases the endocrine activity related to dominance.
- (6) The probability of interaction of an individual  $i$  is an increasing function  $Y_i(F_i)$  of  $F_i$ . This reflects the fact that the probability of interaction increases with rank, and also that ecdysteroids, the titers of which are reflected in  $F$ , may be responsible for aggressive behavior.
- (7) Two individuals  $i$  and  $j$  interact at a frequency that is proportional to the product  $Y_i Y_j$ . This reflects the fact that the frequency of interaction between  $i$  and  $j$  may be related to the time they spend walking on the nest, where interactions take place.

model based on intrinsic initial differences among individuals can explain the data on *Polistes dominulus*.

We will now describe in more detail the self-organization model (Theraulaz *et al.*, 1995; Bonabeau *et al.*, 1996), and discover that the hierarchical structure that this model generates for particular values of the parameters exhibits the properties of the hierarchical structure observed in *Polistes dominulus*, such as the shape of the profile, the stability of the profile in response to the removal of the dominant individual, and the robustness of the profile, which is always obtained irrespective of initial conditions for fixed values of the model parameters. We will use Monte Carlo simulations, in which wasps are represented by agents characterized by a variable,  $F$ , called force.

3.1.2. *Reinforcement.* If two individuals  $i$  and  $j$  engage in a contest, the outcome of the contest is assumed to be probabilistic. Individual  $i$  is dominant over  $j$  with a probability given by

$$Q_{ij}^+ = \frac{1}{1 + e^{-\eta(F_i - F_j)}}, \tag{1}$$

where  $F_i$  is individual  $i$ 's force,  $F_j$  is individual  $j$ 's force, and  $\eta$  is a positive parameter, the meaning of which is discussed below. The probability for  $i$  to lose is equal to the probability for  $j$  to win:

$$Q_{ij}^- = Q_{ji}^+ = \frac{1}{1 + e^{-\eta(F_j - F_i)}} = 1 - Q_{ij}^+. \tag{2}$$

$F_i$  is increased by a constant value ( $\delta^+$ ) in case of victory, and decreased by a constant value ( $\delta^-$ ) in case of defeat. This force can be seen as an indicator of the physiological state of the animal, such as the synthetic activity of the CA, JH and ecdysteroid titers in the hemolymph, or the size of the ovaries. It is part of the model's assumptions to start from the existence of an aggregate variable, denoted by  $F$ , which directly reflects the ability of an individual to dominate in a hierarchical interaction. It is assumed here that  $F_i$  does not depend on which nestmate individual  $i$  is currently facing: the same force value is used to compute the outcome of any contest with any other member of the group. In other words, recognition on an individual basis has no influence and the outcome of a contest depends only on the respective forces of both individuals, as given by equation (1).

$F$  is subject to a feedback mechanism, the sign of which depends on how well an individual with force  $F$  is performing given the current state of the colony's dominance order. When  $\delta^+ = \delta^-$ ,  $F_i$  is simply proportional to the number of times individual  $i$  has been successful minus the number of times it has been dominated.  $F_i$  can in principle take any negative value (for subordinate individuals) or positive value (for dominant individuals).  $F_i$  is bounded by the maximum number of interactions,  $I_{\max}$ , allowed in the simulations. In reality,  $F_i$  may be bounded by

physiological limits: for example, hormonal titers cannot become infinitely large. One may also assume that hierarchical interactions stop whenever an individual's force  $F$  exceeds some threshold, that reflects the unquestionable dominant status of that individual, or the fact that the individual starts laying eggs.

The choice of the sigmoid function in equation (1) is arbitrary, but it is a classic example of a function which combines easy modulation of the deterministic-stochastic aspect with  $\eta$  together with a saturation at large values. When  $F_i - F_j \gg \eta$ ,  $Q_{ij}^+ \approx 1$ . When  $F_i - F_j \ll \eta$ ,  $Q_{ij}^+ \approx 0$ . When  $F_i = F_j$ ,  $Q_{ij}^+ = 1/2$ . In the simulations described in Section 3.1.4,  $\delta^+ = \delta^- = 1$  and  $\eta = 1$ , so that the outcome of a contest is 'almost' deterministic: as soon as  $F_i$  is greater than  $F_j$  by a little more than the minimum amount, which is equal to  $\delta^+$ , individual  $i$  is almost sure to win.

3.1.3. *Probability of interaction.* Let  $P_{ij}$  denote the probability that two individuals  $i$  and  $j$  interact per unit time. We assume that  $P_{ij}$  is given by

$$P_{ij} = Y_i Y_j, \quad (3)$$

where

$$Y_i = \frac{1}{1 + e^{-F_i/\theta}} \quad (4)$$

denotes individual  $i$ 's 'likelihood' to interact with any other individual, and  $\theta$  is an interaction threshold.  $Y_i \approx 1$  when  $F_i \gg \theta$ ,  $Y_i \ll 1$  when  $F_i \ll \theta$ , and  $Y_i = 1/2$  when  $F_i = \theta$ . In the simulation, we set  $\theta$  to 100. In other words, the probability of interaction remains relatively close to 1/2 during the first 100 interactions per individual, the time needed for some individuals to reach a force equal to  $\theta$ .  $P_{ij}$  is a symmetric function of  $i$  and  $j$ , with a value which is maximum when both individuals in the pair are strong, and minimum when both individuals are weak. The middle value taken when a strong individual meets a much weaker one reflects the fact that the strong individual will try to engage in a contest while the weak one will tend to escape, or that the more dominant individual spends more time walking on the nest than its subordinate.

3.1.4. *Results.* In the simulations, identical initial forces are assigned to all individuals: all individuals start in the same state, namely,  $D = 1$ ,  $S = 1$ ,  $F = 0$ ,  $D/D + S = 0.5$ , so that a given individual has an equal probability of winning or being defeated. The total number  $I$  of hierarchical interactions among cofoundresses is initially equal to 0. At each time step, a pair of individuals  $(i, j)$  is randomly selected, and is first tested to determine if  $i$  and  $j$  will interact: this is done according to the probability  $P_{ij}$  [equations (3) and (4)]. If the answer is positive, the total number of interactions  $I$  is incremented by one and individual  $i$  wins with probability  $Q_{ij}^+$ .  $D$  or  $S$  are updated according to the fight's outcome. The simulation stops when  $I$  reaches a predefined maximum number of hierarchical interactions

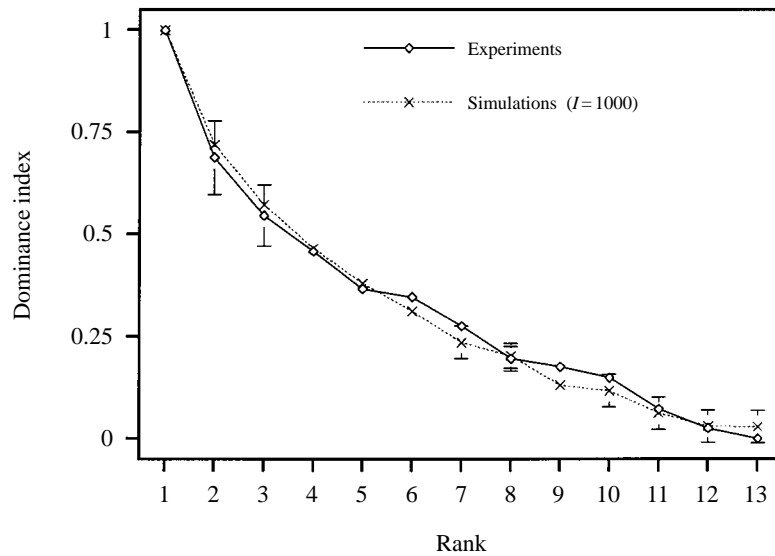


Figure 7. Comparison of the dominance index as a function of hierarchical rank obtained in experiments (same as in Fig. 1) and in Monte Carlo simulations of the self-organization model. Error bars for the curve resulting from the simulations have been obtained by running 20 simulations of  $I = 1000$  interactions for each group of 13 individuals. Parameter values:  $\eta = 5$ ,  $\theta = 100$ ,  $\delta^+ = \delta^- = 1$ .

$I_{\max}$ . Simulations have also been run to study the removal of the dominant individual. When the profile has stabilized, the  $\alpha$ -individual is removed. The model requires the tuning of the parameters  $\eta$ ,  $\theta$ , and  $\delta^+$  (assuming that  $\delta^+ = \delta^-$ ). Since  $\theta$  and  $\eta$  can be scaled in units of  $\delta^+$ , there are really two parameter values to be determined.

Figure 7 shows the hierarchical profile obtained from simulating the model, together with the experimental profile represented in Fig. 1. As can be seen, the simulated profile is difficult to distinguish from the experimental profile. In addition, the obtained profile is robust over experiments, as shown by the small error bars in Fig. 7. As the total number of hierarchical interactions  $I$  increases, the fluctuations, reflected in the error bars, decrease and the profile converges to an extremely stable profile. Figure 8 shows that error bars decrease with increasing  $I$ . For  $I = 10\,000$ , error bars are within the thickness of the line. After 500 interactions, the average profile obtained is already very close to the stable profile, and also to the experimental profile. Note that the experimental profile is always stable after a few hundred interactions.

The final profile is independent of initial conditions. If, instead of starting from initially undifferentiated individuals, forces are assigned to individuals according to a Gaussian distribution, the profile toward which the system converges is unchanged. Initially stronger individuals, however, become higher-ranking individuals, and initially weaker individuals become lower-ranking individuals. Assuming that  $F$

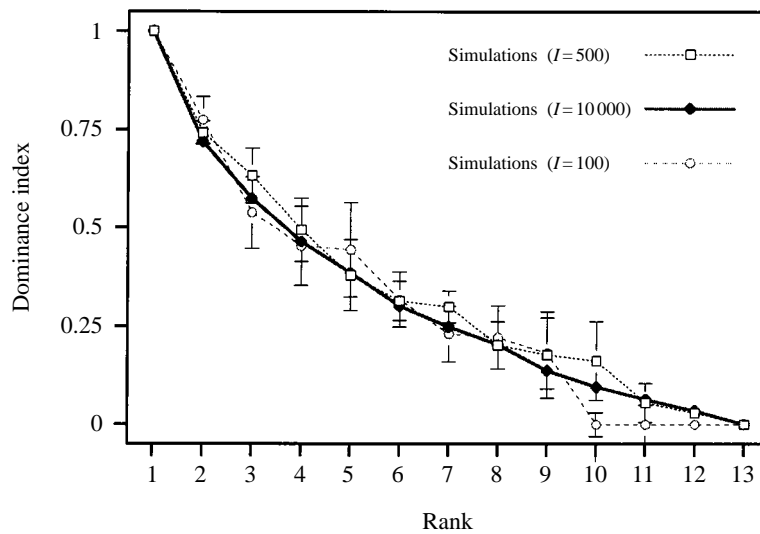


Figure 8. Dominance index as a function of rank obtained from Monte Carlo simulations, for different values of the number  $I$  of simulated interactions:  $I = 100$ , 500, and 10 000. Error bars correspond to averaging over 20 simulations. Same parameter values as in Fig. 7.

grows regularly over time after hibernation in the absence of social interactions, this result is consistent with the observation that emerging early is an advantage to achieve dominant status in a foundress association.

Figure 9 shows the proportion of all dominances and subordinations accounted for by each individual as a function of the individual's rank. This figure is to be compared with Fig. 2. Obviously, the curves are very similar in Figs 9 and 2. The percentage of dominances is characterized by a rapid decay as a function of rank, from 43% (47% in Fig. 2) for the  $\alpha$ -female to 0.02% (0% in Fig. 2) for the female at the bottom of the hierarchy. The percentage of subordinations is first increasing and then decreasing as a function of rank: this is because lower-ranking individuals, although they are almost always defeated, are not involved in many interactions.

The self-organization model generates differentiation between individuals. Figure 10 shows how the forces of the 13 individuals vary with the total number of hierarchical interactions,  $I$ . As can be seen, the force of the dominant individual increases quickly with  $I$ , whereas the forces of its subordinates either decrease, remain in the vicinity of 0, or increase more slowly with  $I$ . The process was stopped at  $I = 500$  interactions. In real foundress associations, it is possible that when  $F$ —for example, hormonal titers—reaches a threshold, the differentiation process stops—for instance when the  $\alpha$ -female starts laying eggs.

The self-organization model is 'endogenous' in that the social organization emerges out of interactions among the females; that is, interactions among the elements of the system itself. But the parameters of the model are certainly influenced by external factors. For example, the probability of interaction between two females depends on the time each of them spends on the nest, which in turn

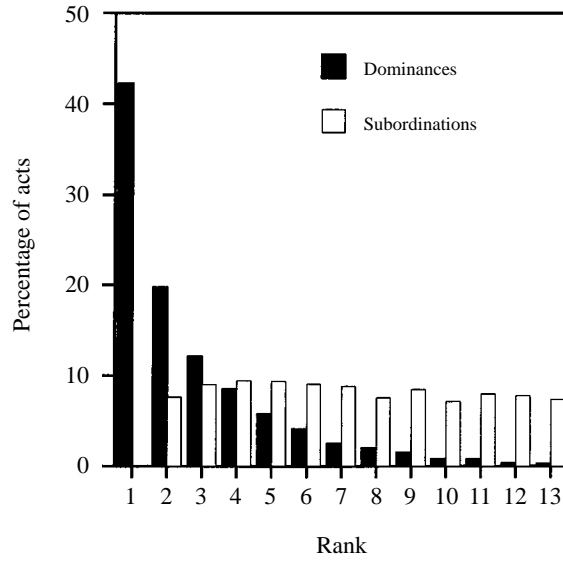


Figure 9. Proportion of dominances and subordinates as a function of hierarchical rank obtained from Monte Carlo simulations of the self-organization model. Same parameter values as in Fig. 7

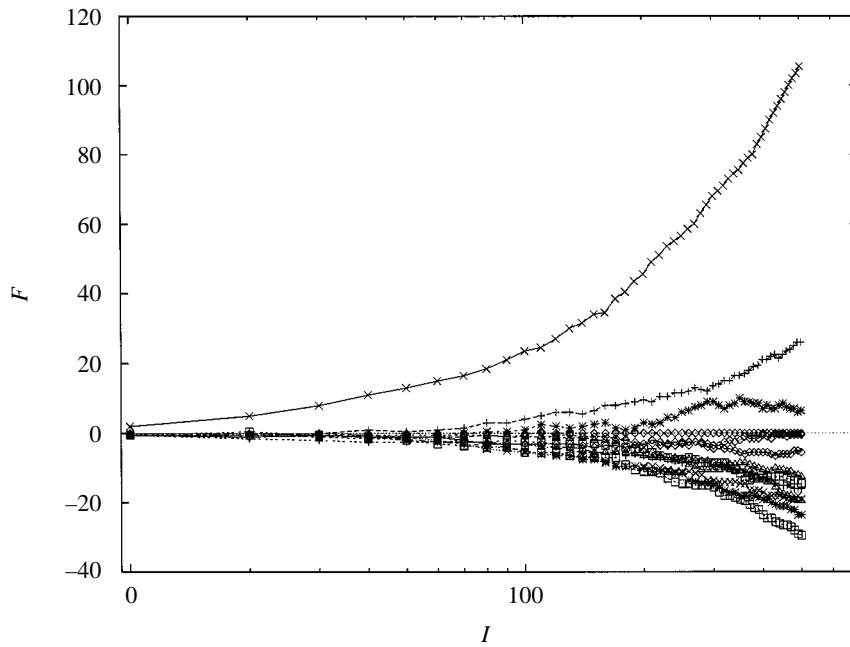


Figure 10. 'Forces' of the 13 individuals simulated with the self-organization model as a function of the number  $I$  of simulated interactions. Same parameter values as in Fig. 7.

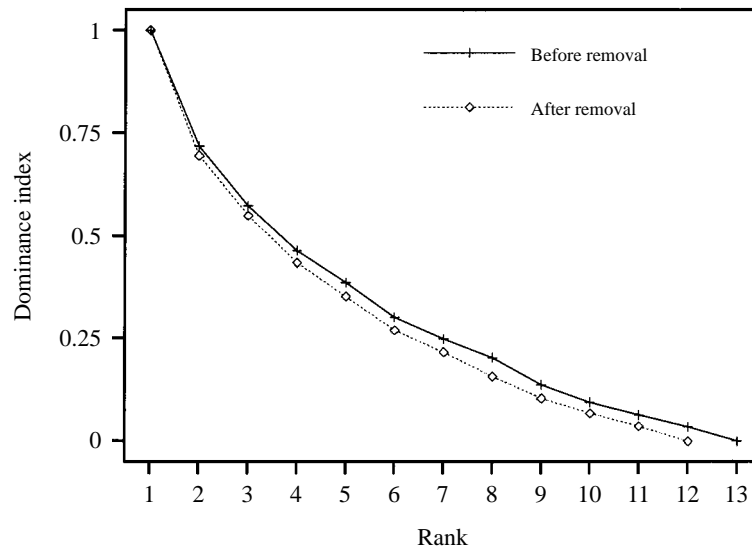


Figure 11. Dominance index as a function of rank before and after the simulated removal of the  $\alpha$  individual in Monte Carlo simulations of the self-organization model. The  $\alpha$  individual was removed after 10 000 simulation steps, and the simulation was then run for another 10 000 steps to obtain the new profile. Same parameter values as in Fig. 7.

depends on how much foraging time is necessary to satisfy colony needs. If food is abundant and easy to find, foragers will spend more time at nest. If food is scarce and hard to find, foragers will spend more time outside the nest. There will be fewer interactions between the dominant and its subordinates, but the amplification effect may be stronger: a subordinate will have to spend more energy foraging, which may lead to diminished ovarian development and lower endocrine activity.

The removal of the  $\alpha$ -individual results in all situations in the reestablishment of the initial hierarchical structure before removal (Fig. 11). A careful study of how ranks change in the simulations after the removal of the  $\alpha$ -individual shows that individuals do not swap ranks in the restructuring process provided initial force differences were sufficiently high: a global shift of the hierarchy is observed. This result is consistent with experiments, in which individuals swapping ranks may be observed in the bottom of the hierarchy, where there is little hierarchical differentiation.

### 3.2. Critique of the self-organization model: an alternative model.

3.2.1. *Critique of the self-organization model.* The self-organization model described in Section 3.1 reproduces the experimental data quite satisfactorily. It goes beyond mere curve fitting in that it reproduces features that do not directly follow from the assumptions. But the assumptions behind the model raise some issues.

- Firstly, it was assumed that self-organization is responsible for the differentiation. But we know that emerging wasps already exhibit initial differences. Can we reproduce the data equally well by assuming that the wasps are already differentiated, without invoking self-organization?
- Secondly, we know that some differentiation takes place after the group has been formed because the ovaries of the  $\alpha$ -female develop while those of the other females tend to stagnate or regress. We know that interactions with subordinates amplify this differentiation. We also know that the production of JH and ecdysteroids is affected by this differentiation. However, this has to do with *reproductive dominance*. Social dominance and reproductive dominance can be separated in experiments with ovariectomized females. Moreover, the respective roles of JH and ecdysteroids are not at all clear. Is the endocrine activity a cause or a consequence of *social dominance*? We do not know whether a reinforcement process also takes place in the context of social dominance. Again, can we reproduce the data by assuming that the wasps are already differentiated, without invoking a further reinforcement process?
- Thirdly, we assumed that the probability of interaction between two individuals  $i$  and  $j$  was given by a function of their abstract forces  $F_i$  and  $F_j$  [equations (3) and (4)].

But we do not know whether the factors that influence the outcome of a fight directly influence the probability of interaction. Indirect effects, such as the spatial distribution of individuals resulting from the division of labor, may explain most of the probability of interaction. One of the problems is that  $F_i$  cannot be measured. Can we construct a model in which the probability of interaction is based on measurable quantities?

The answer to these three questions is yes. An alternative model, a correlational model, the detailed assumptions of which are described in Box 2, can be constructed along the lines suggested by the criticisms.

3.2.2. *Alternative model.* In the alternative model, individuals are assumed to be globally pre-differentiated; that is, initial differences between individuals pre-exist to their first interactions and these differences determine the issue of pairwise contests, leading to a global dominance order. The initial differences are assumed to induce a complete ordering on the set of individuals. Following this assumption, the ordering of the individuals in the dominance hierarchy directly reflects their initial differences. We call this model the correlational model.

For the sake of simplicity, it is assumed that individual  $i$  has rank  $i$ . When two individuals  $i$  and  $j$  interact,  $i$  wins if and only if  $i > j$ . The probability that  $i$  and  $j$  interact is assumed to be proportional to the product of the times they spent walking on the nest. The time spent by  $i$  walking on the nest is assumed to depend solely on its dominance  $X_i$  according to the empirical function  $T(X_i) = 1.32 \times 10^{0.836X_i}$ .

**Box 2****Assumptions of the correlational model**

- (1) Each individual is characterized by a force  $F$ , which influences its ability to win contests.  $F$  reflects endocrine activity, ovarian development, and other factors.
- (2) Individuals have initially different forces, as has been found in nature and experiments. This initial differentiation results from asynchrony in emergence from hibernation, genotypic factors, and differential exposure to environmental signals.
- (3) Individual recognition, if it exists, plays no role in the outcome of a contest. In other words, the force of an individual does not depend on which other individual it is encountering.
- (4) A pairwise contest between  $i$  and  $j$  is won by  $i$  if and only if the force  $F_i$  of  $i$  is greater than the force  $F_j$  of  $j$ . If  $i$  and  $j$  have equal forces, the probability that  $i$  wins is  $1/2$ .
- (5) The probability of interaction of an individual  $i$  is proportional to the time spent by  $i$  walking on the nest, as given by the empirical function  $T(X_i)$  of its dominance index  $X_i$ ,  $T(X_i) = 1.32 \times 10^{0.836X_i}$ .

Note that the correlational model is a *parameter-free* model: all assumptions are based on quantitative experimental observations.

The results obtained with the alternative model are very similar to those obtained with the self-organization model. Figure 12 shows the hierarchical profile obtained from Monte Carlo simulations of the correlational model after  $I_{\max} = 10\,000$  interactions, and compares it with the experimental profile (Fig. 1). The two profiles are very close, and there is not much difference between the profile obtained with the correlational model after  $I = 10\,000$  interactions and the profile obtained with the self-organization model after  $I = 10\,000$  interactions (Fig. 8). But the self-organization model required the tuning of the parameters  $\eta$ ,  $\theta$ , and  $\delta^+$ , whereas the correlational model does not require the tuning of any parameter. Figure 13 shows the fraction of dominances and subordinations of every individual as a function of rank. Figure 13 is almost identical to Fig. 9. More generally, all other properties of the self-organization model are also exhibited by the correlational model (stability of profile over different runs, decrease of fluctuations with increasing  $I$ , robustness with respect to removal of  $\alpha$ -individual), except that the correlational model does not generate differentiation but relies on pre-differentiation. Robustness of the profile with respect to initial conditions is not relevant here, since individuals are pre-ordered at the beginning of each simulation, and that the outcome of a pairwise contest depends only on the rank of both individuals in this pre-order and not on the previous contests of the individuals.

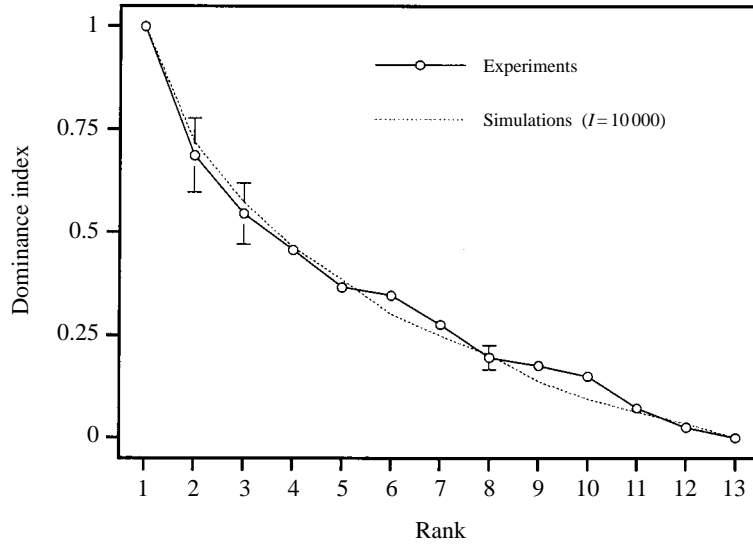


Figure 12. Comparison of the dominance index as a function of hierarchical rank obtained in experiments (same as in Fig. 1) and in Monte Carlo simulations of the correlational model. The curve resulting from the simulations has been obtained by averaging over 20 simulations of  $I = 10\,000$  interactions for each group of 13 individuals. Error bars cannot be distinguished from line thickness.

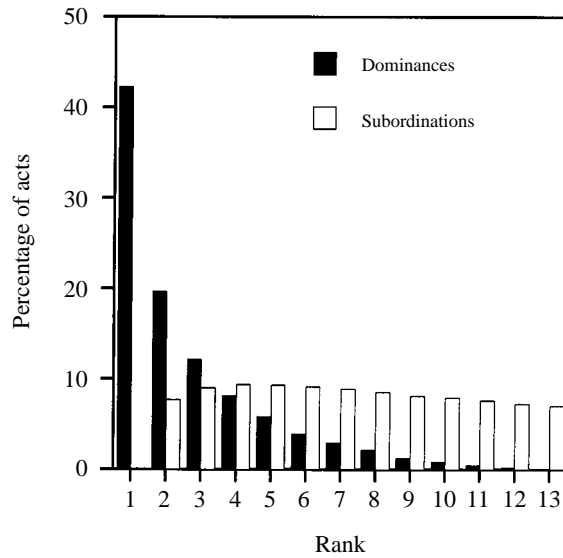


Figure 13. Proportion of dominances and subordinations as a function of hierarchical rank obtained from Monte Carlo simulations of the correlational model.

It seems, therefore, that the correlational model reproduces, and is consistent with, the same experimental data as the self-organization model but with fewer assumptions. Although the correlational model appears more parcimonious than the self-organization model, there still remains to explain why the probability of interaction is given by the function  $T(X(R))$ , described in Section 2.2. It seems that the probability of interaction is the most important factor in determining the shape of the hierarchical profile and the overall pattern of dominances and subordinations. Finally, if the correlational model accounts for the data on social dominance, it cannot describe the kind of differentiation that is observed in the context of reproductive dominance.

#### 4. DISCUSSION

Both the self-organization model and the correlational model are consistent with the available empirical data. The correlational model requires fewer assumptions but only the self-organization model is able to produce differentiation. Which model is right (assuming that one of them is)? Obviously, more experiments are needed to answer this question. In the absence of any further data, the self-organization model is speculative and the correlational model should be preferred. There is no doubt that some form of differentiation takes place in the formation of the *reproductive* dominance order. The fundamental issue is whether there is a parallel differentiation in the formation of the *social* dominance order. Although both types of dominance order are most often associated, and therefore likely correlated, in natural conditions in *Polistes dominulus*, it is not sure that the observation of reproductive differentiation implies the existence of an equivalent social differentiation. And whether there is such a social differentiation, we cannot tell from empirical data. The existence of initial differences between females makes it difficult to look for the contribution of a possible reinforcement process. The physiological correlates of dominance behavior have been shown to be the cause of dominance behavior but they may as well be the effects of dominance behavior through a feedback loop. For example, JH titers determine whether an individual is likely to achieve dominance, but JH titers may be in turn determined by the dominance status of the individual.

Modeling a phenomenon consists not only of fitting existing data with a biologically plausible model; alternative models should also be tested and a careful comparison between the models should point to experiments aimed at discriminating the models. In the present case, the difficulty in discriminating between the models results from the fact that, although the ordering of individuals in the correlational model does not rely on interactions among individuals, such an ordering can only be observed if individuals interact! The only way to find out which model is better is to monitor the physiological correlates of dominance *during* the establishment of a hierarchy. Since measuring hormonal titers and the size of glands requires killing the wasps, this is problematical. But the following experiment would make one step

into that direction. Use groups of individuals of the same age raised in the same laboratory conditions (the idea is to reduce as much as possible the differences that naturally exist between wasps), and measure the relevant variables (hormone titers and volume of CA) at various stages of the formation of a dominance order. Working on ovariectomized females would eliminate the confounding effects of reproductive dominance but may create more problems than it solves, for social and reproductive dominance are tightly coupled. Then, one may study, for example, how the distribution of CA volume changes over time. If the assumptions of the self-organization model are valid, one expects the distribution to be relatively peaked at emergence and to become wider as the number of hierarchical interactions increases because small initial differences become amplified. This distribution could be compared to the distribution obtained with control wasps of the same age raised in isolation. In these latter wasps, the distributions of CA volume and hormone titers are expected to remain peaked, though at a higher level. If such were the case, it would strongly suggest that social interactions are a cause of differentiation by amplification of small differences, a major assumption of the self-organization model. A variation on this experiment consists of systematically plotting the hormone titers and CA volume of an individual as a function of the number of dominances  $D$  and subordinations  $S$  of that individual. If the assumptions underlying the self-organization model are correct, one expects to see a positive correlation (even possibly a linear relationship within some range of values) between  $D-S$  and the measured variables. As regards the probability of interaction, one has to determine whether and how the physiological correlates of dominance influence the probability of interaction. For example, does mobility or the probability of engaging a pairwise interaction increase with JH titers?

Another question of great importance is: how much of a difference between individuals (in terms of CA volume and hormone titers) is needed to obtain a deterministic fight outcome? Indeed, small differences may not affect fight outcome below a certain threshold. If that is the case, one may be able to form groups of individuals with small enough differences that fight outcomes are initially random: only a self-organizing process could then explain the formation of a clear-cut dominance order. One way of measuring the effect of differences is to form pairs of wasps, observe the outcome of the first interaction and sacrifice the players to measure CA volume and hormone titers. With a sufficiently large number of pairs, one could titrate the effects of physiological differences on the outcome of dominance interactions. When differences are large, the outcome should be predictable: the female with the larger values dominates. As differences between members of a pair become small, however, there may come a point at which the outcome of the interaction is random.

The self-organization model has been invoked to explain the emergence of the hierarchical structure in bumblebees *Bombus terrestris* (Van Honk and Hogeweg, 1981; Hogeweg and Hesper, 1983, 1985) and primates (Hemelrijk, 1996), but in both cases empirical evidence is too weak to justify the assumptions of the model.

Recent experiments on crayfish *Astacus astacus* are promising (Huber and Delago, 1999; Gössmann and Huber, 1999). When juvenile crayfish are put together, they engage in pairwise contests that may only rarely involve the unrestrained use of the claws. Gössmann and Huber (1999) studied five groups of five crayfish in which a linear dominance order always emerged, and observed that: (1) reversals in position are common early after the formation of the group but their number decreases significantly over time; (2) the propensity to engage in fights is a function of rank, irrespective of the identity of the individual that has that rank, with the more dominant crayfish being more likely to start fights; (3) the first fights determine the final rank; (4) dominance relationships become polarized, with higher-ranking individuals growing more dominant and lower-ranking individuals becoming more subordinate; and (5) ranks may change from day to day, influenced by the outcomes of contests early in the day. Although these observations are not sufficient to support the self-organization model, they suggest that it *may* apply. Studies that show that the neuromodulator serotonin plays an important role in regulating aggression in crayfish shows that it might be possible to elucidate the neurophysiological basis of that behavior (Huber *et al.*, 1997; Huber and Delago, 1999).

## 5. CONCLUSION

We have presented two alternative models for the formation of a hierarchical structure in *Polistes dominulus*: a self-organization model, in which small differences between individuals are amplified by a double-reinforcement process and that produces differentiation, and an alternative model, where initial differences between individuals are sufficient to explain the data related to social dominance. Experiments have been suggested to distinguish these two alternative explanations. It is likely, however, that both explanations coexist. Small differences that exist between individuals are sufficient to explain the social dominance data, but the amplification of these small differences may be the only way to explain the organization of the reproductive dominance order:

At the end of hibernation differences in the endocrine activity even exist between the foundresses from the same hibernation site (Röseler, 1985). The small differences in the beginning become more and more pronounced during colony development by inhibition of subordinate females as well as by the trophic advantage and lessened external activities of the  $\alpha$ -female. This system originally postulated by Pardi (1946) for ovary development ensures the reproductive exclusiveness of the  $\alpha$ -female. (Röseler *et al.*, 1984, p. 141).

From an evolutionary perspective, the combination of both mechanisms—predetermination and self-organization—is satisfactory because the reinforcement process makes differentiation robust and ensures a proper partitioning of reproduction. If post-hibernation differences between two females are too small to determine a

winner and a loser consistently over time, none of the females will become dominant or subordinate in the absence of a reinforcement process. Successive encounters will produce a sequence of wins and losses for each individual.

#### ACKNOWLEDGEMENT

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